Strong cycles show boom-and-bust lifestyle for snowshoe hares

by Ed Berg

Last week's Refuge Notebook reviewed the ups and downs of central Kenai snowshoe hare populations since 1983. Snowshoe hares have been down since 2001 and now are just beginning to climb out of their long low phase toward their next peak, according to our annual counts of hare fecal pellets at five sites.

Snowshoe hares have a strong population cycle that runs 9-11 years in many places, and more like 12-14 years on the Kenai. For animals with well-defined population cycles, there are two basic questions: first, why do they cycle? And second, why are their cycles so regular? These are two very different questions, and in this article I'll address the first question about what causes hares to flourish for several years and then become scarce for a period of years. In a future article I'll review the evidence for the hare cycle being synchronized by the 11-year sunspot cycle.

Life is not easy for snowshoes hares. They are truly everybody's favorite prey species, and experience 70% mortality per year. That is, only 30% of the hare population survives from one year to the next, and this is in the good years. To offset this mortality they have to "breed like rabbits," typically having 1-4 litters per year, with up to 14 leverets (babies) per litter (the average is 5).

The traditional explanation for the snowshoe hare cycle is that, as hare numbers increase, so do the numbers of one of their predators, the lynx. Supposedly the lynx numbers increase to the point that they over eat the hares, then the hare population crashes, and the lynx population crashes a year or two thereafter. With few lynx around, the hare population will begin to rebuild and the cycle repeats itself.

Canadian researchers conducted a series of clever experiments over a period of 20 years (including two hare cycle peaks) in the Kluane area of the Yukon to test this and other explanations. They set up 1-square kilometer experimental plots, where they could count hares by catch-and-release methods or use radio-collars. Two of the plots were fenced with a wire mesh large enough to let hares in and out, but electric wires excluded large mammalian predators like lynx

and wolves. On two unfenced plots the experimenters provided as much food (rabbit chow and spruce tops) as the hares could eat. Three plots were controls where the hares were simply counted, with no food or fencing.

More hares were initially attracted to the free food in the unfenced plots, as might be expected, but during the crash phase of the hare cycle when predators were abundant, the hare population declined sharply at the same rate as in the control plots. This showed that the hare cycle in Kluane is not driven by food shortage. The hares were not in any way starving to death; they were simply being eaten by increased numbers of predators.

On the Kenai, by contrast, we suspect that the decrease in hardwood browse in our post-fire maturing forests does at least retard the recovery of hares from the low phase. Like Kluane we don't see starving hares in the winter, but our hare pellet census plots are located in maturing old burns (of 1947 and 1969) and they certainly suggest declining peak phase hare populations compared to anecdotal reports of higher hare peaks in the early days of these large burns.

One of the Kluane electric fence plots was provided with free food, but the other had no added food. During the crash phase the hares in the plot with both fence and food survived best of all the plots, but their numbers still decreased to only 20% of their peak phase numbers. Hares on the unfenced food plots declined to about 5% of their peak phase numbers, so the fence did help somewhat but not a lot.

One lesson of this study is that there are more predators involved than simply lynx. Red squirrels were effect predators on the leverets. Hawks, goshawks, and owls, as well as lynx and coyotes were important predators of juveniles and adults.

The fenced pens could exclude the lynx and coyotes but not the birds. The fenced pens with and without free food both saw declines in hare survival rate, although the hares in the free food pen didn't decline quite as much. This suggests that well-fed hares are better able to escape avian predators.

Most interesting to me in this study are the "psychological" aspects. It turns out at stress is a major player in the hare cycle. Bunnies are sensitive creatures, which probably comes as no surprise to anyone who has ever raised rabbits. Stress effects first appear when the female hares' reproductive output begins to drop just as the population cycle begins its upswing (such as on the Kenai right now).

An Alberta study showed, for example, that the average number of leverets dropped from 17 to 15 during the first three years of the population increase phase, and then dropped more sharply to eight leverets during the final two years before the population peaked. In the Kluane study survival of both adults and nursing juveniles also began to decline as soon as the population started to increase, before the predators arrived in large numbers.

These effects suggest to me that social interactions among the hares (like crowding and competition) may have been the main source of stress during the early years of the population increase, and then there is a shift to fear of predation as the number of predators increase.

Whatever the cause of the stress, it permanently marked the mothers. The researchers captured fe-

male hares at both the low and peak phases of the population cycle, and raised them in cages for five to seven years under very benign conditions (free food, no crowding, etc.). The peak phase females never recovered their full fertility; even in the third year of captive breeding the peak phase females had less than half the number of offspring as the low-phase females. It must have been hare hell at the peak of the cycle!

These studies in Kluane and the Kenai show that a variety of predators (in addition to lynx), stress, and in some cases food supply all play a role in the hare cycle, but probably acting in different ways and different degrees in different areas. We can imagine such factors affecting many other kinds of animals and causing fluctuations of their numbers, for example moose, fish, and human beings. The remarkable thing about snowshoe hares is the regularity of their cycle, which is more-or-less synchronized all across boreal North America. But that is a story for another day...

Ed Berg has been the ecologist at the Kenai National Wildlife Refuge since 1993. He thanks Ted Bailey for assistance in writing this article. Previous Refuge Previous Refuge Notebook columns can be viewed on the Web at http://www.fws.gov/refuge/kenai/.